



Passalidae (Coleoptera: Scarabaeoidea) of the Greater and Lesser Antilles

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Abstract

We present a synthesis of the state of knowledge concerning the species of Passalidae (Coleoptera) of the West Indies and we present a key to the species. The recently described genus *Antillanax* Boucher renders the subgenus *Passalus* (*Pertinax*) Kaup paraphyletic, therefore we place *Antillanax* in synonymy with *Passalus* (*Pertinax*) and we propose a new combination for *Passalus* (*Pertinax*) *doesburgi* (Boucher). The island richest in species is Hispaniola, with five species, three of them endemic. Excluding Trinidad and Tobago, the passalid fauna of the West Indies comprises 13 species; this is low richness, but with high endemism (50%), especially for the Greater Antilles.

Key words: bess beetles, West Indies, biodiversity, new species

Resumen

Se sintetiza el conocimiento de las especies de Passalidae (Coleoptera) presentes en las Antillas y se presenta una clave para las especies. La descripción reciente del género *Antillanax* Boucher vuelve parafilético al subgénero *Passalus* (*Pertinax*) Kaup; por tanto, se propone la sinonimia de *Antillanax* con *Passalus* (*Pertinax*) y una nueva combinación para *Passalus* (*Pertinax*) *doesburgi* (Boucher). La isla más rica en especies es La Española, con cinco especies, tres de ellas endémicas. Excluyendo Trinidad y Tobago, la fauna de Passalidae de las Antillas está constituida por 13 especies; lo que indica un nivel de riqueza bajo, pero con alto grado de endemismos (50%), especialmente en las Antillas Mayores.

Introduction

Passalidae is principally a pantropical group that is represented in the Neotropics by the tribes Proculini and Passalini. These tribes include approximately 420 species (Reyes-Castillo & Ibáñez 2008), the majority of which live in rotting tree trunks. Excluding Trinidad and Tobago, which are traditionally considered to be part of the South American continental platform islands (Peck *et al.* 2002), Proculini do not occur the Antilles. Passalini is represented by few species compared with similar continental areas, but with high endemism, especially in the Greater Antilles.

The first reference of passalids in the Antilles was by Palisot de Beauvois (1805) who described *Paxillus pentaphyllus* Palisot de Beauvois from Hispaniola. Later, *Passalus affinis* Percheron and *Passalus dominicanus* van Doesburg were described (both endemic to Hispaniola), as well as *Passalus pertyi* (Kaup) (endemic to Cuba). Leng & Mutchler (1914) cited 25 species for the Antilles, including Trinidad and Tobago. Nevertheless, 12 of these species correspond to invalid synonyms and various records were rejected later. Hincks & Dibb (1935) registered 16 species for the Antilles, excluding many of the synonyms of Leng & Mutchler (1914) list. Since then, various

works have cited passalid species from the Antilles, especially Chalumeau & Gruner (1974) for the French Antilles, Cartwright & Chalumeau (1978) for Dominica, Reyes-Castillo *et al.* (1995) for Hispaniola, Peck *et al.* (2002), Peck (2006, 2009, 2010) for the Lesser Antilles and Galindo-Cardona (2003) for Puerto Rico. Nevertheless, in the majority of published works, specimens were not studied and the authors only cite records from previous publications.

Chalumeau (1983), Reyes-Castillo *et al.* (1995), Boucher (2005) and Galindo-Cardona (2003) indicate that the records of various continental species for the Antilles are due to errors that have confounded the passalid composition of the Antilles. In what is perhaps the most important compendium of Antilles Passalidae, Ivie & Gillogly (1998) present a checklist indicating the reasons for rejecting various previously cited species, based as well on previous rejections proposed by Chalumeau (1983) and Reyes-Castillo *et al.* (1995), leaving only nine of the 16 species that Hincks & Dibb (1935) had cited.

In this paper, we strengthen the results of Ivie & Gillogly (1998), showing diagnoses of the Antilles passalid species, citing specific localities, and including a species identification key.

Methods

We examined 343 specimens from the collections of the Royal Institut de Sciences Naturelles de Belgique (RISNB); the Instituto de Ecología, Xalapa, Mexico (IEXA), the Universidad del Valle de Guatemala (UVGC), and The Field Museum of Natural History, Chicago, Illinois, United States of America (FMNH). We did an exhaustive literature search for Antilles passalids. For each species we include a diagnosis, material examined, and commentaries. In the taxonomic treatment and morphological terminology we follow Boucher (2005), except for male genitalia where we follow Reyes-Castillo (1970).

Results

A total of 28 passalid species have been recorded for the Antilles; however, eight of the records are of continental species that we doubt are found in the Antilles. Including Trinidad and Tobago, the Antilles passalid fauna consists of 20 species: 17 Passalini and 3 Proculini (Table 1). Trinidad and Tobago have more than a dozen species, all broadly distributed in South America. Excluding Trinidad and Tobago, the Antilles possess only 13 species, all from the tribe Passalini. The richest island, Hispaniola, has five species including three endemics.

As occurs in South America, *Passalus* is the dominant genus, with 10 of the 13 Antilles species. Six species of *Passalus* are endemic to the Antilles, most of the subgenus *Pertinax*. The subgenus *Passalus* is represented by five species widely distributed in South America and one species from Dominica, Saint Lucia, and Martinique. The only species of *Spasalus* recorded from the Antillies is also widely distributed in South America. The two species of *Paxillus* are endemic, one each from Hispaniola and Jamaica.

Tribe Passalini

Passalus (*Passalus*) *abortivus* Percheron, 1835

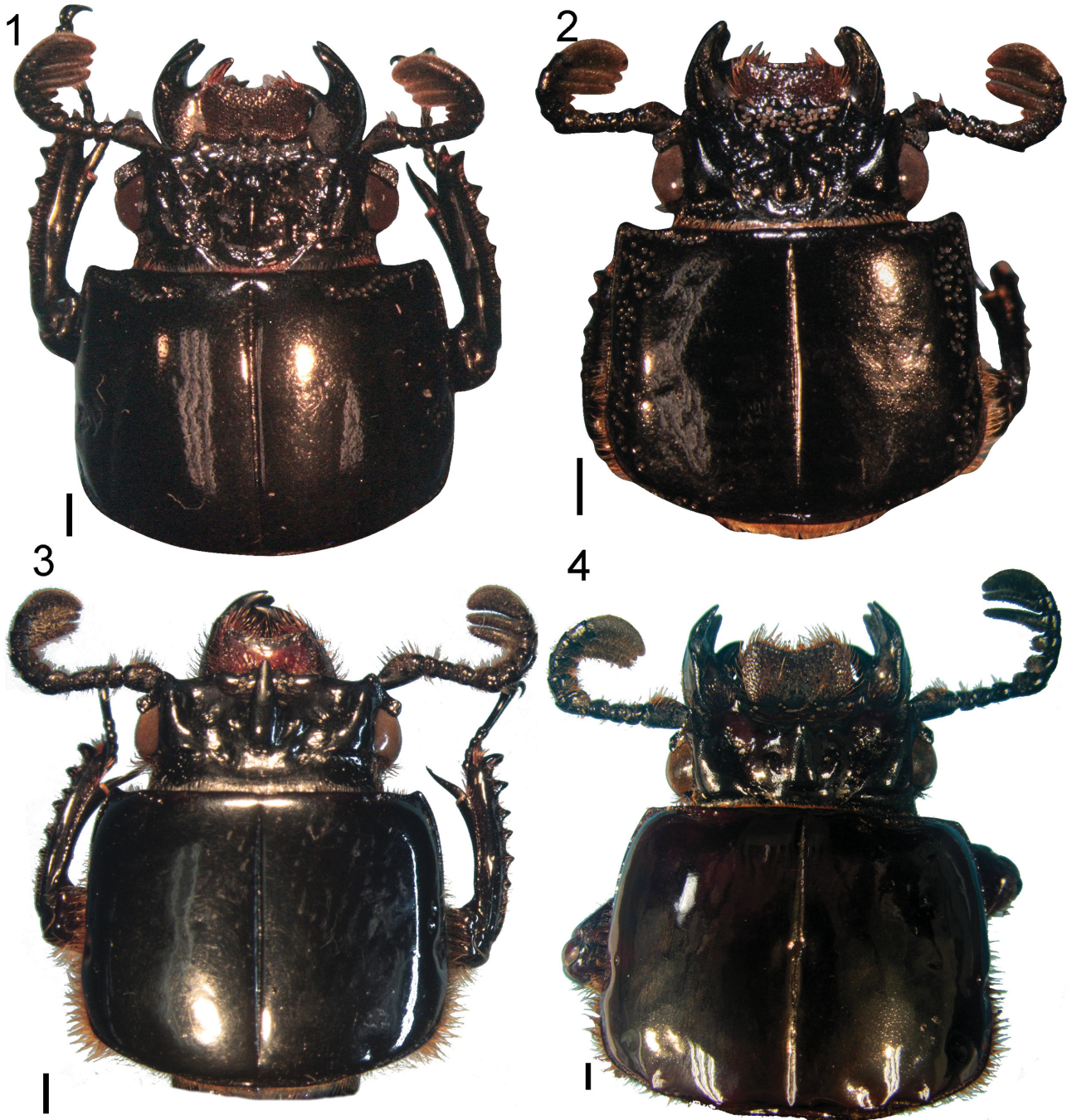
(Fig. 1)

Type locality. Unknown (Percheron 1835).

Diagnosis. 28.2–30.6 mm total length. Clypeus hidden below frons, not visible dorsally, with anterior angles developed. Frons border with two secondary median-frontal teeth united basally. Frontal fossae pubescent. Medial-frontal tubercles developed; internal tubercles large, not united by a ridge to the medial-frontal tubercles, located at half the distance between the median frontal structure (MFS) and the medial-frontal tubercles. Central tubercle of MFS with apex not free, basolateral tubercles marked. Antennal club trilamellate. Apex of lacinia bidentate. Medial-basal mentum elevated and glabrous. Prosternal process rhomboidal, angled sharply. Mesosternal scar (as defined in Reyes-Castillo 1970) pubescent, marked, and oval. Metasternum pubescent anterolaterally and in lateral groove; disc delimited by punctures from posterior to middle. Humeri pubescent, epipleura pubescent basally.

Material examined. Two specimens. TRINIDAD AND TOBAGO: Trinidad: Arima-Blanchisseuse Rd. Simla Research Station, collected at mercury vapor light, 10°42'N 61°17'W, 800', 22.V–3.VI.2000 Kriska, Katovich (1 UVGC); Asa Wright Nature Ctr. 7.5 mi N. of Arima on Blanchisseuse Road. 21.VI.1984, P.J. Clausen, *Passalus abortivus* Perch. Det.: JCS 2002 (1 UVGC).

Distribution. Brazil, Colombia, French Guiana, Guyana, Peru, Suriname, Trinidad and Tobago, and Venezuela, (Luederwaldt 1931, Reyes-Castillo 1973, Amat-García *et al.* 2004).



FIGURES 1–4. Head and pronotum, dorsal view. 1. *Passalus abortivus*. 2. *P. bucki*. 3. *P. coarctatus*. 4. *P. interruptus*. Scale bars: 1 mm.

***Passalus (Passalus) bucki* Luederwaldt, 1931**

(Fig. 2)

Type locality. Brazil.

Diagnosis. 34 mm total length. Clypeus hidden below frons, not visible dorsally, with anterior angles developed. Frons border with two secondary mediofrontal teeth separated by a distance slightly less than the distance separating the secondary mediofrontal tooth from its respective mediofrontal tooth. Frontal fossae glabrous. Medio-frontal tubercles developed, on their exterior side at base are the interior tubercles that are same size as medio-frontal tubercles. Central tubercle of MFS with apex not free, basolateral tubercles marked. Antennal club tetralamellate, with the fourth lamella reduced. Apex of lacinia bidentate. Mentum with medial base swollen and glabrous. Prosternal process rhomboidal, truncate. Mesosternum glabrous with scars marked and elongate. Antero-lateral metasternum and lateral groove pubescent, disc delimited by punctures posterior to middle. Humeri pubescent, epipleura pubescent in basal third.

Material examined. One specimen. TRINIDAD AND TOBAGO: Trinidad, St. Andrew County, 2.5 mi. E of Valencia, ex large (very hard) logs on ground, coll. P. Hunter, W.T. Atyeo, 27.III.1987, *Passalus (Passalus) bucki* Lued. Reyes-Castillo det. 87 (1♂ IEXA).

Distribution. Argentina, Brazil, Colombia, French Guiana, and Trinidad and Tobago (Luederwaldt 1931, Hincks & Dibb 1935, Reyes-Castillo 1973, Amat-García *et al.* 2004, Jiménez-Ferbans *et al.* 2013).

Comments. This species is sometimes confused with *P. interstitialis*, from which it differs by its smaller size and the elytral pubescence that only covers the basal third of the epipleura and the tenth interstriae. Also, the basolateral prothorax has less dense pubescence than *P. interstitialis*.

***Passalus (Passalus) coarctatus* Percheron, 1835**

(Fig. 3)

Type locality, Brazil

Diagnosis. 34.9–38.3 mm total length. Clypeus hidden below frons, not visible dorsally, with anterior angles developed. Frons border with two secondary mediofrontal teeth separated by a distance slightly less than the distance separating the secondary mediofrontal tooth from its respective mediofrontal tooth. Frontal fossae glabrous. Medio-frontal tubercles developed, basolaterally with interior tubercles that are smaller. Central tubercle of MFS with apex very free, basolateral tubercles. Antennal club trilamellate. Apex of lacinia bidentate. Mentum with medial base swollen and pubescent. Prosternal process rhomboidal, acute. Mesosternum pubescent with scars not marked. Antero-lateral mesosternum and lateral groove pubescent, disc delimited by punctures except anteriorly. Humeri pubescent, epipleura pubescent in the basal two-thirds.

Material examined. 12 specimens. TRINIDAD AND TOBAGO: Trinidad: Arima Valley, Log 7"dia., 580 m, 19.XII.1981, J.C. Schuster. *Passalus unicornis*// *Passalus (Passalus) coarctatus* Percheron, 1835 Det.: Jiménez-Ferbans, 2012 (5 UVGC); St. Andrew County, 2.5 mi. E of Valencia, ex. Large (very hard) logs on ground, 27.III.1987, coll. P. Hunter, W.T. Atyeo, *Passalus (Passalus) unicornis* Lep. et Serv. Reyes-Castillo, det. 87// *Passalus (Passalus) coarctatus* Percheron, 1835 Det.: Jiménez-Ferbans, 2012 (1♀, 1♂ IEXA); George County mountains, 7 mi. N Port of Spain, ex decaying log, 26.III.1987, coll: P. Hunter, W.T. Atyeo. *Passalus (Passalus) unicornis* Lep. et Serv. Reyes-Castillo, det. 87// *Passalus (Passalus) coarctatus* Percheron, 1835 Det.: Jiménez-Ferbans, 2012 (2♀♀, 2♂♂ IEXA). St. George Co., Simla Research Station, Arima Valley, N. Range, 800 ft. 10°41'34"N 61°17'22"W, 23.v.2000, Alistair S. Ramsdale (1 UVGC).

Distribution. Brazil, Trinidad and Tobago (Percheron, 1835).

Comments. The prominent central tubercle of *P. coarctatus* causes confusion with *P. unicornis*; however, *P. coarctatus* has 8–10 glabrous elytral striae, medial basal region of mentum pubescent, and mesosternal scar pubescent. Another similar species is *P. coniferus* Eschscholtz, from which *P. coarctatus* differs by having a very free central tubercle.

***Passalus (Passalus) interruptus* Linnaeus, 1758**

(Fig. 4)

Type locality. "America" (=New World).

Diagnosis. 44.2–50.9 mm total length. Clypeus hidden below frons, not visible dorsally, with anterior angles developed. Frons border with two secondary mediofrontal teeth separated by a distance slightly less than the distance separating the secondary mediofrontal tooth from its respective mediofrontal tooth. Frontal fossae glabrous. Medio-frontal tubercles developed, basolaterally with interior tubercles that are same size as medio-frontal tubercles. Central tubercle of MFS with apex slightly free, basolateral tubercles marked. Antennal club trilamellate. Apex of lacinia bidentate. Mentum with medial base swollen and glabrous. Prosternal process rhomboidal, acute. Mesosternum pubescent or glabrous with scars marked and elongate. Antero-lateral mesosternum and lateral groove pubescent, disc delimited by punctures excluding apex. Humeri pubescent, epipleura pubescent in basal third. Incomplete marginal groove in last abdominal sternite.

Material examined. 28 specimens. TRINIDAD AND TOBAGO: Trinidad: Arima Valley, 800–1200 ft. 10–22.II.1964, coll. Rozen, Wygodzinsky, *Passalus (Passalus) interruptus* (Linneo) Reyes-Castillo, det. 1971 (4 IEXA); Arima Valley, ASA Wright Nature Center, 1300 feet, 25.VI.1984, col. L. Harris, *Passalus (Passalus) interruptus* (Lin.) Reyes-Castillo, det. 87 (1 IEXA); George County mountains, 3 mi. N Arima, ex decaying log, 24.III.1987, coll. P.E. Hunter, W.T. Atyeo, *Passalus (Passalus) interruptus* (L.) Reyes-Castillo, det. 87 (2♀♀, 3♂♂ IEXA); same data as before, 7 mi. N Arima (1♀ IEXA); same data as before, 6 mi. N Arima (2♂♂ IEXA); George County mountains, 7 mi. N Port of Spain, ex decaying log, 26.III.1987, coll. P.E. Hunter, W.T. Atyeo, *Passalus (Passalus) interruptus* (L.) Reyes-Castillo, det. 87 (1♀, 1♂ IEXA); Port of Spain, 21.VIII.1966. J. Geijskes, *Passalus (Passalus) interruptus* (Linneo) Reyes-Castillo, det. 1971 (1 IEXA); Port of Spain, 1910 (1 IEXA); St. Andrew County, near Sangre Grande, ex decaying log (called "Pummarac" tree), 27.III.1987, coll. P. Hunter, W.T. Atyeo, *Passalus (Passalus) interruptus* (L.) Reyes-Castillo, det. 87 (7♀♀, 4♂♂ IEXA).

Distribution. From Panama to Argentina and Trinidad and Tobago (Reyes-Castillo 1973).

Comments. Recorded from Tobago by Peck *et al.* (2002) as *Passalus* cf. *interruptus*. This species some times is confused with *P. punctiger*, but is distinguished by its larger size and incomplete marginal groove in last abdominal sternite.

***Passalus (Passalus) interstitialis* Eschscholtz, 1929**

(Fig. 5)

Type locality. Rio Janeiro, Brazil.

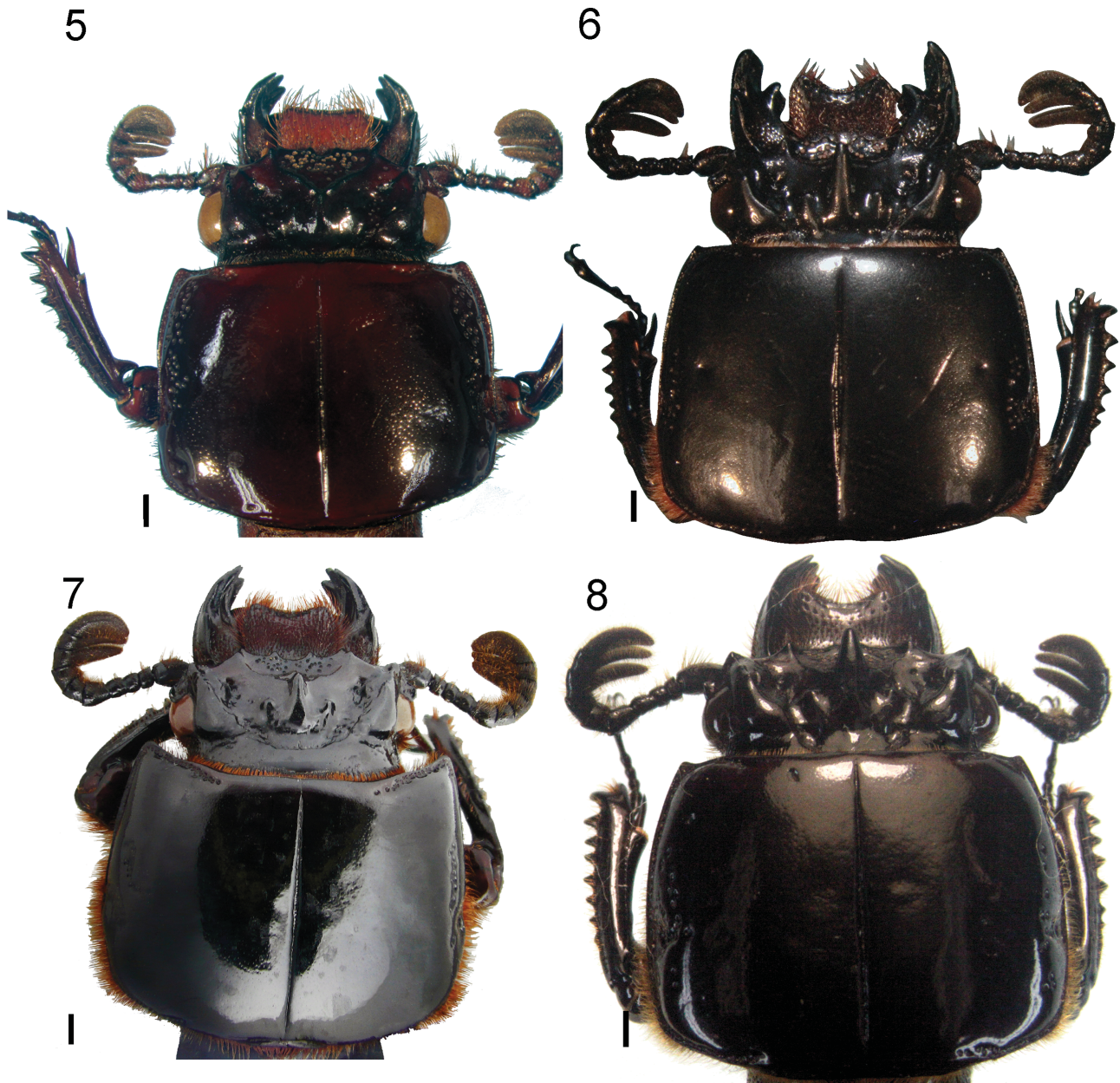
Diagnosis. 29.0–34.0 mm total length. Clypeus hidden below frons, not visible dorsally, with anterior angles developed. Frons border with two secondary mediofrontal teeth separated by the same distance separating the secondary mediofrontal tooth from its respective mediofrontal tooth. Frontal fossae glabrous. Medio-frontal tubercles small, basolaterally with large interior tubercles. Central tubercle of MFS with apex not free, basolateral tubercles marked. Antennal club tetralamellate. Apex of lacinia bidentate. Mentum with medial base swollen and glabrous. Prosternal process rhomboidal, truncate. Mesosternum glabrous with scars marked and elongate. Antero-lateral mesosternum and lateral groove pubescent, disc delimited by punctures excluding apex. Humeri pubescent, epipleura pubescent in two basal third.

Material examined. 26 specimens. CUBA: Prov. Artemisa, Municipio San Cristóbal, Sierra del Rosario, Finca El Cuabalito, 25.II.2012, col. E. Pardi (2 IEXA). GRENADA: Par. St. Andrew, Pearls Airport, 7.vi.1990, M.C. Thomas/ Under bark of hog plum log (2 UVGC). JAMAICA: Bath, 12.VIII.1967, leg. W. Klopp, *Passalus (Passalus) interstitialis* Esch. Det.: Jiménez-Ferbans 2015 (1 FMNH); same data, 14.VIII.1967 (1 FMNH); same data, 22.VIII.1967 (1 FMNH). Nr. Ewarton. Polyground, E.A. Woodruff Collection, coll. Davenport (3 IEXA); Mandeville, Manchester Par., on doorstep in morning at Howard Franks house, 24.VI.1970, col. P. Drummond (1 IEXA); Mandeville, Collected at light, 20.V.1958, MW Sanderson, *Passalus (Passalus) interstitialis* Esch. Det.: Jiménez-Ferbans 2012 (1 IEXA); Morant Bay, 28.X.73, Laniz? (1 IEXA); Norant Bay, 28.X.73, Comb., (1 IEXA); 5 mi W Port Antonio, Under Bark, 8.XII.1975, col. C.W. O'Brien (6 IEXA); Portland Parish, 8 miles N on rd. from Ecclesdown. 3.16.1969, coll. Peter Drummond (1 IEXA). TRINIDAD & TOBAGO: Trinidad: Arima Valley, 800–

1200 ft., 5–15.II.1965, J.G. Rozen collector (1 IEXA); same locality as before, 22.II.1964, coll. Rozen & Wygodzinsky (1 IEXA); N. Range, Arima-Blanchisseuse Rd., Textel, nr. Morne Bleu 2300, 7.5.1985. C.W. & L.B. O'Brien, *Passalus (Passalus) interstitialis* Esch. Det.: Jiménez-Ferbans 2012 (3 UVGC).

Distribution. From Mexico to Argentina (Hincks and Dibb 1935, Reyes-Castillo 1973) and Cuba, Grenada, Jamaica, and Trinidad and Tobago (Arrow 1907, Reyes-Castillo 1973, Ivie & Gillogly 1998, Peck *et al.* 2002).

Comments. Sometimes confused with *P. punctiger*, *P. interstitialis* differs by its smaller size, flattened body, and apex of central tubercle not free. Specimens from Jamaica are larger than the maximum size of 29 mm reported Reyes-Castillo (1973) for French Guiana specimens. Morffe *et al.* (2009) and Morffe & García (2010, 2011) described new species and a new genus of Hystrignathidae (Nematoda) parasite from *P. interstitialis*.



FIGURES 5–8. Head and pronotum, dorsal view. **5.** *Passalus interstitialis*. **6.** *P. trinesides*. **7.** *P. punctiger*. **8.** *P. unicornis*. Scale bars: 1 mm.

Passalus (Passalus) punctiger LePeletier & Serville, 1825
(Fig. 7)

Type locality. Cayenne, French Guiana.

Diagnosis. 31.5–38.3 mm total length. Clypeus hidden below frons, not visible dorsally, with anterior angles developed. Frons border with two secondary mediofrontal teeth separated by an equal or slightly less distance than the distance separating the secondary mediofrontal tooth from its respective mediofrontal tooth. Frontal fossae glabrous. Medio-frontal tubercles developed, with larger interior tubercles. Central tubercle of MFS with apex little free, basolateral tubercles marked. Antennal club trilamellate. Apex of lacinia bidentate. Mentum with medial base swollen and glabrous. Prosternal process rhomboidal, truncate. Mesosternum glabrous with scars marked and elongate. Antero-lateral mesosternum and lateral groove pubescent, disc delimited by punctures excluding apex. Humeri pubescent, epipleura pubescent in basal third.

Material examined. 17 specimens. SAINT VINCENT: South River, 30.IV.1978, Posion, Paratype, *Pass. punctiger arrowiella* n. ssp. Det. F. Chalumeau 78 (1 IEXA); Delaway, 31.X.1977, Chalumeau, Paratype, *Passalus punctiger arrowiella* Chalum. det. F. Chalumeau 78 (1 IEXA). TRINIDAD AND TOBAGO: Little Tobago, 15.III.1942, Col & pres by Henry Field, *Passalus punctiger* St. Farg. det.: F.S. Pereira 1959 (2 FMNH). Trinidad: ?VI.1929, Col. By S. Haweis, Pres. By Miss Becky White, *Passalus punctiger* St. Farg. det.: F.S. Pereira 1959 (1 FMNH); Brickfield, 15.III.1947, CHNM-Trinidad Zool. Expedition, F. Wonder leg., *Passalus punctiger* St. Farg. det.: F.S. Pereira 1959 (1 FMNH). St. Andrew County near Sangre Grande, ex palm tree logs on ground, 27.III.1987, cols. P. Hunter, W.T. Atyeo, *Passalus (Passalus) elfriedae* Lued. Reyes-Castillo, det. 1987, *Passalus (Passalus) punctiger* Lep. et Serv. det.: Jiménez-Ferbans 2012 (3♂♂ IEXA); same locality, date and collectors, ex decaying log called "Pummarac" tree (2♀♀ IEXA); George County mountains 7 mi. N Port of Spain, ex decaying log, 26.III.1987, cols P. Hunter, W.T. Atyeo, *Passalus (Passalus) punctiger* Lep. et Serv. Reyes-Castillo, det. 87 (2 IEXA); George County mountains 7 mi. N Port of Spain, ex decaying log, 6.III.1987, cols P. Hunter, W.T. Atyeo, *Passalus (Passalus) punctiger* Lep. et Serv. Reyes-Castillo, det. 87 (2♀♀, 1♂ IEXA); George County near Sangre Grande, ex decaying log called "Pummarac" tree, 27.III.1987, cols. P. Hunter, W.T. Atyeo, *Passalus (Passalus) punctiger* Lep. et Serv. Reyes-Castillo, det. 87 (1♂ IEXA).

Distribution. From the United States of America to Argentina and Grenada, Jamaica, Saint Vincent and the Grenadines, and Trinidad and Tobago (Reyes-Castillo 1973, Chalumeau 1978, Schuster 1978, Peck *et al.* 2002, Peck 2010).

Comments. Ivie & Gillogly (1998) did not report this species, despite citing some papers of Chalumeau, who described *Passalus punctiger arrowiella* from Saint Vincent (Chalumeau 1978). Luederwaldt (1931), Reyes-Castillo (1973) and other authors have cited *P. punctiger* from Cuba; however, only Luederwaldt (1931) has cited specimens from this island as "Museu Berlin-Dahlem: Paraguay, Cuba (Coll. Kraatz)"; thus, its presence in Cuba must be confirmed.

***Passalus (Passalus) unicornis* LePeletier & Serville 1825**

(Fig. 8)

Type locality. Cayenne, French Guiana.

Diagnosis. 36.6–45.0 mm total length. Clypeus hidden below frons, not visible dorsally, with anterior angles developed. Frons border with two secondary mediofrontal teeth contiguous at base or separated by a distance slightly less than the distance separating the secondary mediofrontal tooth from its respective mediofrontal tooth. Frontal fossae glabrous. Medio-frontal tubercles developed. Interior tubercles equal size to medio-frontal tubercles, located on the base of the exterior side of medio-frontal tubercles. Central tubercle of MFS with apex very free, reaching anterior border of frons; basolateral tubercles marked. Antennal club trilamellate. Apex of lacinia bidentate. Mentum with medial base swollen and glabrous. Prosternal process rhomboidal, truncate. Mesosternum glabrous with scars marked and elongate. Antero-lateral metasternum and lateral groove pubescent, disc delimited by punctures excluding apical edge. Humeri pubescent, epipleura pubescent in most of its length.

Material examined. 42 specimens. DOMINICA: Saint Andrew, 3.VIII.1973. Camb. leg. (1 IEXA). GUADELOUPE: Guadeloupe, 1968, P. Gallichet leg. (11 IEXA); Grand Fond S.A., 20.VIII.1977, F-C. M. Chalumeau, leg., *Passalus (Passalus) unicornis* Lep. et Serv., 1825 Reyes-Castillo, det. 80 (2 IEXA); Neuf Château, Ste. Marie, 1.VII.1971, col. L. Gruner, *Passalus (Passalus) unicornis* Lep. et Serv., 1825 det.: Jiménez-Ferbans, 2012 (12 IEXA); Sofaia, 285 m, 3.XII.1982, J.C. Schuster, *Passalus unicornis* (15 UVGC). Morne Louis, 660 m, 3.XII.1982, J.C. Schuster, *Passalus unicornis* LeP. et Serv. det.: Jiménez-Ferbans, 2013 (1 UVGC).

Distribution. Brazil, Colombia, Dominica, French Guiana, Guadeloupe, Martinique, Saint Lucia, Trinidad and Tobago (Percheron 1835, Luederwaldt 1931, Chalumeau & Gruner 1974, Chalumeau 1978, Cartwright & Chalumeau 1978, Ivie & Gillogly 1998, Peck *et al.* 2002, Peck 2006).

Comments. Hunt (1981) described four new Nematoda from the midgut caeca of *P. unicornis* from Saint Lucia. Schuster (1992) recorded *P. unicornis* from Trinidad and Guadeloupe; however, the specimens cited by Schuster (1992) from Trinidad were actually *P. coarctatus*.

***Passalus (Passalus) trinesides* Boucher, 2015**

(Figs. 6, 9)

Type locality. Martinique.

Diagnosis. 40.5–41.6 mm total length. Clypeus hidden below frons, not visible dorsally, with anterior angles developed, of same size as medio-frontal tubercles. Frons border with two secondary mediofrontal teeth contiguous at base or light separated. Frontal fossae glabrous and smooth or with two punctures. Medio-frontal tubercles small, projected forward. Internal tubercles as large as medio-frontal tubercles, projected upward and located close to mediofrontal tubercles. Central tubercle of MFS with apex free, reaching anterior border of frons; basolateral tubercles marked. Antennal club trilamellate. Apex of lacinia bidentate. Mentum with medial base swollen and glabrous. Prosternal process rhomboidal, truncate. Mesosternum glabrous; mesosternum scar elongate, well defined, rugose. Anterolateral metasternum and lateral groove pubescent, disc delimited by punctures excluding apical edge. Humeri pubescent, epipleura pubescent in most of its length.

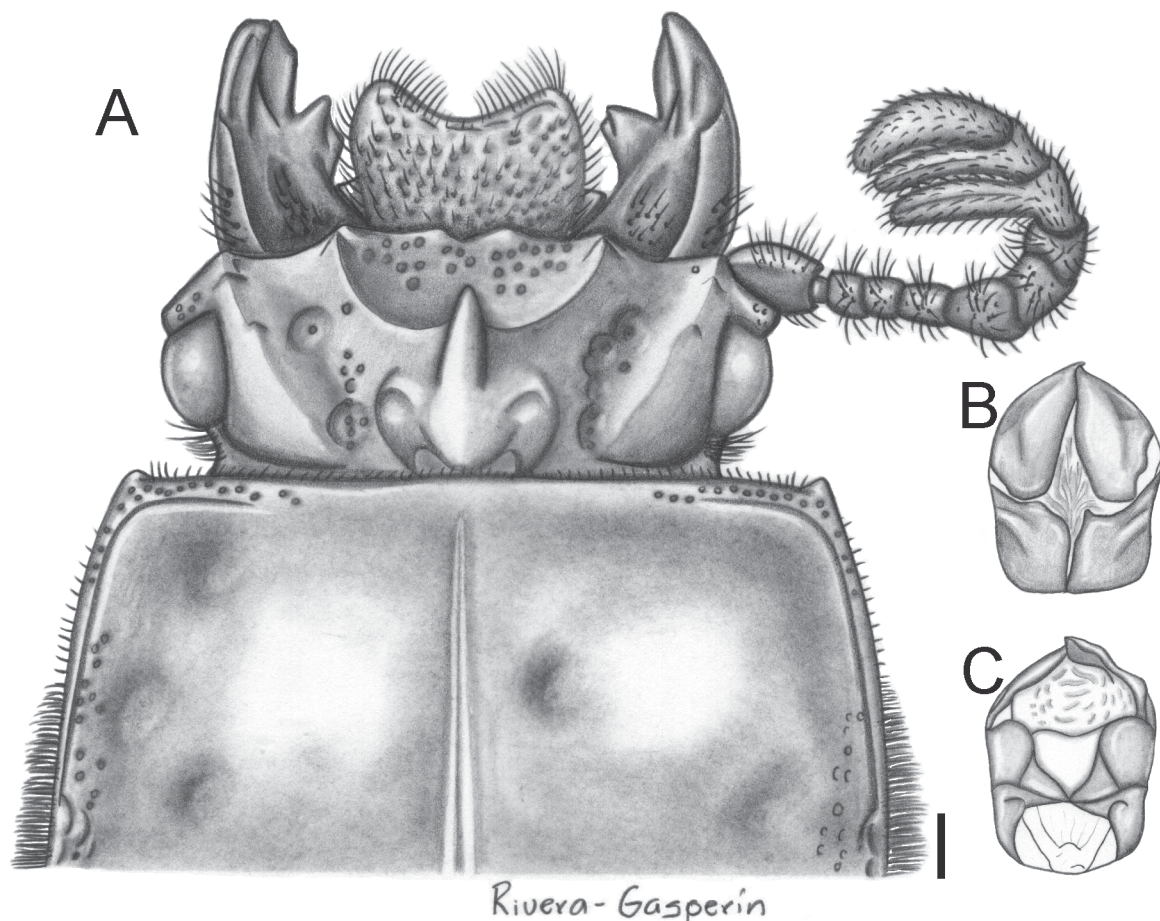


FIGURE 9. *Passalus trinesides*. (A) Head and anterior part of pronotum. (B) Aedeagus, ventral view. (C) Aedeagus, dorsal view. Scale bar: 1 mm.

Material examined. 15 specimens. DOMINICA: Saint Andrew, 3.VIII.1973. Camb. [Camberfort] leg. (3 IEXA); Salibia, 30.I.1968, leg. B. Malkin, *Passalus unicornis* det.: J.C. Schuster, *Passalus* (*Passalus*) *trinesides* Boucher det.: Jiménez-Ferbans, 2015 (1 FMNH); Pont Cassé, 1900', 19.VI.2004, CW. & L.B. O'Brien (1 IEXA). MARTINIQUE: Coll. R.I.Sc.N.B., *Passalus* (*Passalus*) *unicornis* Lep. et Serv., 1825 Reyes-Castillo, det. 88 (1 RISNB); Pont de l'Alma, 12.V.1960, Collectors P. & C. Vaurie, *Passalus* (*Passalus*) *unicornis* Lepeletier et Serville Reyes-Castillo, det. 1970 (1 IEXA). SAINT LUCIA: 17.XII.1911, Col. & Pres. by A.F. Porter, *Passalus unicornis* det.: FS. Pereira, 1959, *Passalus* (*Passalus*) *trinesides* Boucher det.: Jiménez-Ferbans, 2015 (8 FMNH).

Distribution. Dominica, Martinique, and Saint Lucia.

Passalus (*Pertinax*) *affinis* Percheron, 1835

(Fig. 10)

Type locality. Santo Domingo, Dominican Republic.

Diagnosis. 42.5–48.6 mm total length. Clypeus hidden below frons, not visible dorsally, with anterior angles developed. Frons border straight, with or without a strong notch. Frontal fossae glabrous. Medio-frontal tubercles developed, basolaterally with smaller interior tubercles. Central tubercle of MFS with apex not free; basolateral tubercles large and marked. Antennal club trilamellate. Apex of lacinia bidentate. Mentum with medial base swollen and glabrous. Prosternal process rhomboidal, acute. Mesosternum glabrous with scars marked and elongate. Antero-lateral metasternum and lateral groove pubescent, disc delimited by punctures posterior to middle. Humeri pubescent, epipleura pubescent in basal third.

Material examined. 33 specimens. CNHM 1955, Karl Brancsik Colln. Ex Eduard Knirsch. *Passalus affinis* det.: F.S. Pereira 1959 (1 FMNH). DOMINICAN REPUBLIC: Boca Chica 10 Km, 21.X.1972, J. & S. Klapperich, *Passalus* (*Pertinax*) *affinis* Percheron, Reyes-Castillo, det. 1974 (1 IEXA); Barahona Province, Polo, 13.IX.1973, J. Schuster, *Passalus* (*Pertinax*) *affinis* Perch. Det. J.C.S. 1985 (1♀ UVGC); Cambita Garabitos (S.C.), 3.VII.1978, Col. Fc et Bud, Cambefort leg., *Passalus* (*Pertinax*) *affinis* Percheron. Reyes-Castillo, det. 80 (5 IEXA); Dominican Republic, no further data. (1 UVGC); col., Muerto en terrario VIIa, J. Schuster (1 IEXA); Muerto en terrario VIIa, J. Schuster (2 IEXA); El Seibo Prov., 8 km W Miches, cacao plantation, 16.IX.1973, J. Schuster (2 UVGC); same locality and collector, cacao plantation and large trees 15,16.IX.1973 (5♀♀, 4♂♂ 5 gender unknown UVGC); La [H]ermita. El Cercado Prov., 28.III.1981, Abud-L., Marcano Cols., M.N.H.N., *Passalus affinis* Det. Maes 1995 (1 IEXA). HAITI: Dept. du Sud, 14 Km N. of Cavaillon, 1800 ft, 6.VIII.1962, coll. D.R. Paulson, Woodruff Colección, *Passalus* (*Per.*) *affinis* Perch. 1835. S. Boucher det. 1987. (2 IEXA); Lebrun, moist log, 2.I.1974, coll. R.L. Sette. *Passalus* (*Pertinax*) *affinis* Perch. Det.: J.C.S. 1985 (1 UVGC); Port-Au-Prince, Muséum Paris, *P. affinis* Percheron 1835 S. Boucher det. 93 (1 IEXA).

Distribution. Endemic to Hispaniola (Reyes-Castillo *et al.* 1995, Ivie & Gillogly 1998).

Comments. Schuster (1975) described the copulation and aedeagus of this species. Schuster and Reyes-Castillo (1981) described the larvae based on specimens from Barahona and El Seibo (cited as “El Ceibo”).

Passalus (*Pertinax*) *antillarum* (Arrow, 1907)

(Fig. 11)

Type locality. Grenada: Windsor, Chantilly, and Grand Etang.

Diagnosis. 20.5–22.5 mm total length. Clypeus hidden below frons, not visible dorsally, with anterior angles well developed, larger than medio-frontal tubercles. Frons border with weak notch, without secondary medio-frontal tubercles. Frontal fossae glabrous. Medio-frontal tubercles developed, not joined to interior tubercles. Internal tubercles as large as medio-frontal tubercles. Central tubercle of MFS with apex not free; basolateral tubercles weak. Antennal club trilamellate, with short lamellae. Apex of lacinia bidentate. Mentum with medial base swollen and glabrous. Prosternal process rhomboidal, acute. Mesosternum glabrous with scars marked and elongate. Antero-lateral metasternum and lateral groove glabrous, disc delimited by sparse punctures in posterior area. Humeri and epipleura glabrous.

Material examined. Nine specimens. GRENADA: no more locality data, xi–xii.1912, R. Thaxter (1 UVG).

Saint Andrew Parish: Grand Etang, 8.I.1969, col.: R.T. Bell/ *Passalus (Pertinax) antillarum* (Arrow) Schuster Det. 2003 (1 IEXA; 1 UVGC); same locality, 12.I.1969, col.: R.T. Bell/ *Passalus (Pertinax) antillarum* (Arrow) Reyes-Castillo, det. 82 (1 IEXA); same data as anterior/ *Passalus (Pertinax) antillarum* (Arrow) Schuster Det. 1981 (2 UVGC); Rd. end to Mt. St. Catherine, 23.ii.1990, at night, in rotting log, R.E. Woodruff, A. Thomas, J. Telesford (1 UVGC). Saint David: Mt. Sinai, 20.xii.1981, Chalumeau (2 UVGC).

Distribution. Grenada (Arrow 1907, Hincks & Dibb 1935, Ivie & Gillogly 1998).

Comments. Arrow (1907) cited Windsor, Chantilly, and Grand Etang as the type locality. Hincks & Dibb (1935), Blackwelder (1944), and Ivie & Gillogly 1998 only cited Arrow (1907), without recording any specimens. Therefore, the specimens cited in this paper are the only specimens known other than the type series. We consider this species as endemic to Grenada, being the only endemic passalid to the Lesser Antilles.



FIGURES 10–13. Head and pronotum, dorsal view. 10. *Passalus affinis*. 11. *P. antillarum*. 12. *P. dominicanus*. 13. *P. latifrons*. Scale bars: 1 mm.

***Passalus (Pertinax) dominicanus* van Doesburg, 1953**

(Fig. 12)

Type locality. Santo Domingo, Dominican Republic.

Diagnosis. 27.9–30.56 mm total length. Clypeus hidden below frons, slightly visible dorsally, with anterior angles well developed, larger than medio-frontal tubercles. Frons border with notch, without secondary medio-frontal tubercles. Frontal fossae glabrous. Medio-frontal tubercles developed, not joined to interior tubercles. Internal tubercles larger than medio-frontal tubercles. Central tubercle of MFS with apex not free; basolateral tubercles weak. Antennal club trilamellate, with short lamellae. Apex of lacinia bidentate. Mentum with medial base swollen and glabrous. Prosternal process rhomboidal, acute. Mesosternum glabrous without scars. Antero-lateral metasternum pubescent and lateral groove glabrous, disc delimited by sparse punctures in posterior area. Humeri glabrous and epipleura with sparse setae in basal area.

Material examined. Nine specimens. DOMINICAN REPUBLIC: La Vega, Constanza, 12.VII.1978 Chalumeau, *Passalus (Pertinax) dominicanus* V. Doesburg Reyes-Castillo, Det. 1993 (1 IEXA); La Vega, 20.IX.1973, col. J. Schuster (1 IEXA); La Vega PR. 3 km E Jima, 7.V.1985, coll E. Giesbert (1 UVGC); S.W. of La Vega. 20-IX-1973, J. Schuster, *Passalus (Pertinax) dominicanus* det.: J. Schuster (3♀♀, 3♂♂ UVGC).

Distribution. Endemic to Hispaniola (Reyes-Castillo *et al.* 1995, Ivie & Gillogly 1998).

Comments. Schuster (1983) described two kinds of sounds produced by adults of this species in three behavioral contexts. Boucher (2005) analyzed the homoplastic character state of clypeus dorsal exposure among *P. dominicanus* and the Proculini.

***Passalus (Pertinax) latifrons* Percheron, 1841**

(Fig. 13)

Type locality. Guyane.

Diagnosis. 29.3–30.8 mm total length. Clypeus hidden below frons, not visible dorsally, with anterior angles developed, larger than medio-frontal tubercles. Frons border with weak notch, without secondary medio-frontal tubercles. Frontal fossae glabrous. Medio-frontal tubercles not developed, not joined to interior tubercles. Internal tubercles small and located between medio-frontal tubercles and central tubercle. Central tubercle with apex not free; basolateral tubercles small but marked. Antennal club trilamellate, with short lamellae. Apex of lacinia bidentate. Mentum with medial base swollen and glabrous. Prosternal process rhomboidal, acute. Mesosternum glabrous with scars weak or absent. Antero-lateral metasternum and lateral groove glabrous, disc delimited by sparse punctures in posterior area. Humeri and epipleura glabrous.

Material examined. Six specimens. TRINIDAD AND TOBAGO: Tobago: Forest Preserved, Bloody Bay Rio, log 9'x2', 470 m, J.C. Schuster, 13.XII.1981 (2 UVGC). Trinidad: Arima Valley, xii.1981, Simlazo/ 800 ft. alt., #TT-20 alone, J.C. Schuster (1 UVGC); 1 mi. S Maracas Beech 500' 6.VIII.1963, col. E. Kjellesvig-Waering, *Passalus (Pertinax) latifrons* Perch. Reyes-Castillo det. 1985 (1 IEXA); George County mountains 7 mi. N Port of Spain, 26.III.1987, ex decaying log cols. P. Hunter, W.F. Atyeo, *Passalus (Pertinax) latifrons* Perch. Reyes-Castillo det. 1987 (1 IEXA); Lopinot Valley, Devil Hole, 24.II.1967, J.P.E.C. Darlington (1 FMNH).

Distribution. Brazil, French Guiana, Peru, Suriname, and Trinidad and Tobago, (Reyes-Castillo 1973, Schuster 1992). Kuwert (1891) recorded this species from Colombia and Cuba; but later (Kuwert 1898), only cited Guyana. We consider the record from Cuba to be erroneous.

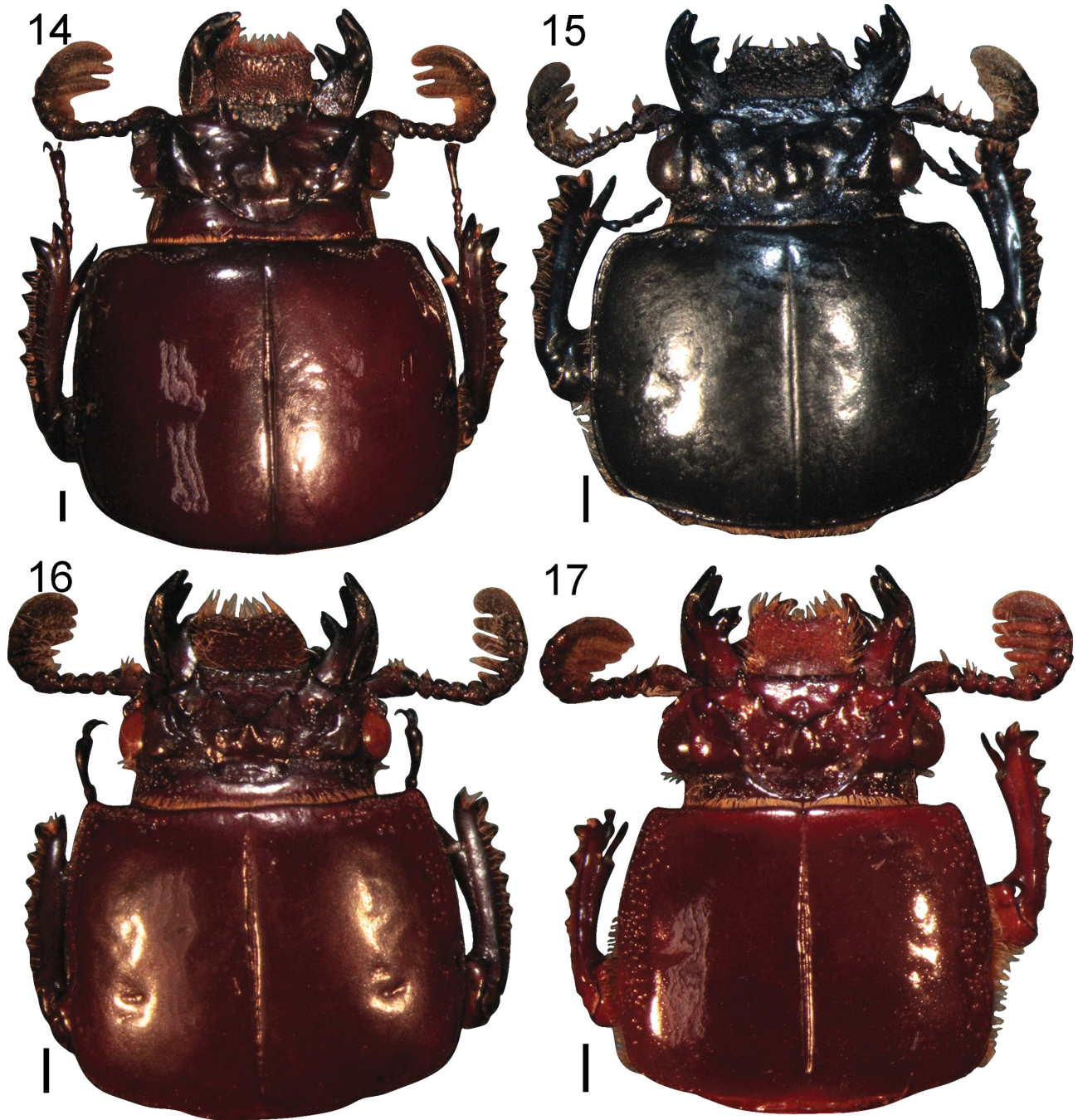
***Passalus (Pertinax) pertyi* (Kaup, 1869)**

(Fig. 14)

Type locality. Cuba.

Diagnosis. 39.5–40.9 mm total length. Clypeus hidden below frons, not visible dorsally; anterior angles well developed, larger than medio-frontal tubercles. Frons border with weak notch, without secondary medio-frontal tubercles. Frontal fossae glabrous. Medio-frontal tubercles not developed, not joined to interior tubercles. Internal

tubercles small and located between medio-frontal tubercles and central tubercle. Central tubercle with apex not free; basolateral tubercles small but marked. Antennal club trilamellate, with large lamellae. Apex of lacinia bidentate. Mentum with medial base swollen and glabrous. Prosternal process rhomboidal, acute. Mesosternum glabrous with scars weak or absent. Antero-lateral metasternum and lateral groove glabrous, disc delimited by sparse punctures in posterior area. Humeri and epipleura glabrous.



FIGURES 14–17. Head and pronotum, dorsal view. 14. *Passalus pertyi*. 15. *Passalus doesburgi*. 16. *Paxillus jamaicensis*. 17. *Paxillus pentaphyllus*. Scale bars: 1 mm.

Material examined. 16 specimens. CUBA: CNHM 1955, Karl Brancsik Colln. Ex Eduard Knirsch/ *Passalus affinis* det.: F.S Pereira 1959/ *Passalus (Pertinax) pertyi* (Kaup, 1869) det.: Jiménez-Ferbans, 2015 (1 FMNH); Upper Yara Valley, 18-20.x.??/ T.P.R.F. Ent. No 3512/ Feeding in rotten logs/ I.C. Scaramuzza, coll./ *Passalus pertyi* Kaup Det. Hincks & Dibb (1 UVGC). Prov. Artemisa, Municipio San Cristóbal. Sierra del Rosario, Finca El Cuabalito, 25.2.2012, col. E. Pardi (3 IEXA); Prov. Camagüey, Monte Imias nr. California, at light, 7.VI.1959, col. M.W. Sanderson, *Passalus (Pertinax) pertyi* Kaup. Reyes-Castillo det. 80 (1 IEXA); Guantánamo, Collection Le

Moult. Coll. R.I.Sc.N.B., *Passalus (Pertinax) pertyi* Kaup. Reyes-Castillo det. 1985 (2 RISNB); La Habana, Le Moult Vendit. Coll. R.I.Sc.N.B., *Passalus (Pertinax) pertyi* Kaup. Reyes-Castillo det. 85 (5 RISNB); Topas, St. Spiritus, coll. Escambray. 3-1987 Col.: Grillo, *Passalus pertyi* Det. Maes '95, ADN 0045 (1 IEXA); Cuba/ *Pertinax pelliculatus*/ *Passalus (Pertinax) pertyi* Kaup. Reyes-Castillo, det. 87 (1 IEXA); 13 40 [green circular label]/ *Passalus (Pertinax) pertyi* Kaup 1869. S. Boucher det. 1987 (1 IEXA).

Distribution. Endemic to Cuba (Reyes-Castillo *et al.* 1995, Ivie & Gillogly 1998).

Comments. Reyes-Castillo *et al.* (1995) commented the erroneous citation from Hispaniola by Hincks & Dibb (1935). García *et al.* (2009) and Morffe & García (2011) described a species and genus of Hystriognathidae (Nematoda) parasitizing *P. pertyi*. Notwithstanding that Peck (2005) cited *P. convexus* Dalman as widespread in Cuba, we consider this to be erroneous. The specimens used were probably misidentified *P. pertyi*.

***Passalus (Pertinax) doesburgi* (Boucher, 2015) new combination**

(Figs. 15, 18)

Type locality. Dominican Republic.

Material examined. 10 specimens. DOMINICAN REPUBLIC: Pedernales, Las Abejas, 38 km NNW Cabo Rojo, 18°09'N, 71°38'W, Robert L. Davidson 1160m 13-July-1987 // *Passalus (Pertinax) dominicanus* van Doesburg det.: J. Schuster 1987 Lacks prominent internal tubercles (1♀ UVGC); Prov. Pedernales, Pedernales, Las Abejas, Sierra Bahoruco 27.VI.1989, M.N.H.N., col.: Matusik-Guerrero, 34956, *Passalus dominicanus* det. Maes '95 (1♀ IEXA); Pedernales, Las Abejas, Sierra Bahoruco 18-28.VI.1989, leg. Matusik // *Passalus (Pertinax) dominicanus* det. A.R. Gillogly, 1998 // *Passalus (Pertinax) doesburgi* (Boucher) det.: Jiménez-Ferbans, 2015 (8 FMNH).

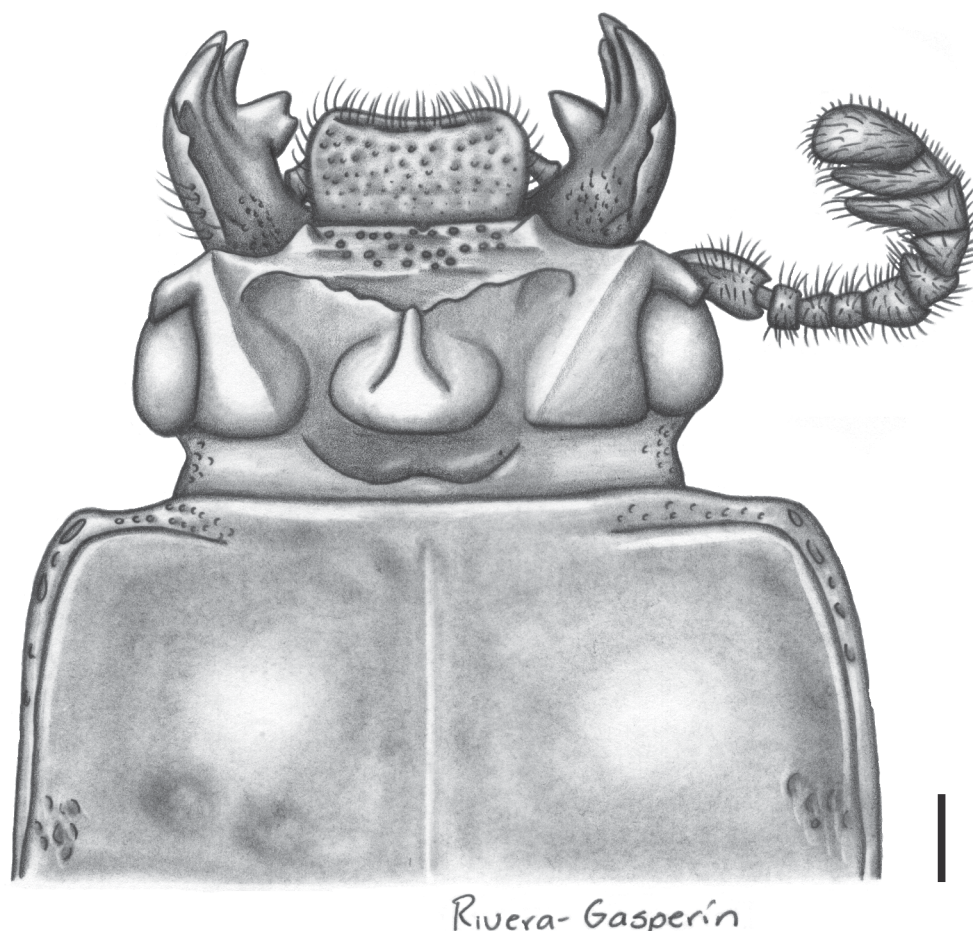


FIGURE 18. *Passalus doesburgi* head and anterior part of pronotum. Scale bar: 1 mm.

Diagnosis. 26.6–28.4 mm total length. Clypeus hidden below frons, slightly visible dorsally, with anterior angles well developed, larger than mediofrontal tubercles. Frons border with notch, without secondary mediofrontal tubercles. Frontal fossae glabrous. Mediofrontal tubercles developed, not joined to interior tubercles. Internal tubercles smaller than mediofrontal tubercles. Central tubercle of MFS with apex not free; basolateral tubercles weak. Antennal club trilamellate, with short lamellae. Apex of lacinia bidentate. Median basal region of mentum protruding and pubescent posteriorly. Prosternal process rhomboidal, acute. Mesosternum glabrous without scars. Anterolateral metasternum and lateral groove glabrous, disc delimited by punctures in posterior area. Humeri and epipleura glabrous.

Distribution. Dominican Republic, from mid-altitudes of Sierra Bahoruco, an area dominated by cloud forest (Cámara 2004).

Comments. Boucher (2015b) described the genus *Antillanax* Boucher for the species *Passalus dominicanus*, *P. pertyi*, and *P. doesburgi*. However, Boucher (2015b) stated “Following the phylogenetic advances on the Passalini, *Antillanax* is a possible relict of the “*Pertinax* lineage” in the Greater Antilles”. This is somewhat congruent with the cladogram of Jiménez-Ferbans & Reyes-Castillo (2014), where *Passalus dominicanus* and *P. pertyi* are nested within *Passalus (Pertinax)*, and related to *P. convexus*. Since the genus *Antillanax* renders the subgenus *Passalus (Pertinax)* paraphyletic, we hereby place *Antillanax* in synonymy with *Passalus (Pertinax)*.

***Paxillus jamaicensis* Hincks, 1950**

(Fig. 16)

Type locality. Jamaica.

Diagnosis. 27.2–29.7 mm total length. Clypeus hidden below frons, not visible dorsally, with anterior angles slightly developed. Frons border straight, without secondary medio-frontal tubercles, sometimes with weak notch. Frontal fossae glabrous. Medio-frontal tubercles developed, joined to interior tubercles by a ridge. Internal tubercles smaller than medio-frontal tubercles. Central tubercle with apex not free; basolateral tubercles small but marked. antennal club with five lamellae, first lamellae reduced. Apex of lacinia unidentate. Mentum with medial base flat and glabrous. Prosternal process pentagonal. Mesosternum glabrous with wide scars. Antero-lateral metasternum and lateral groove glabrous, disc entirely delimited by punctures. Humeri pubescent and epipleura glabrous.

Material examined. 14 specimens. JAMAICA: Cumberl Dist. Clarendon, 15-18.XII.1919, about 3000 ft, *Paxillus jamaicensis* Hincks Reyes-Castillo, det. 88 (1 IEXA); Ecclesdown, 21.VII.60, P. & G. Vaurie, *Paxillus jamaicensis* Hincks Reyes-Castillo, det. 88 (1♀, 1♂ IEXA); Portland Parish. Hardwar Gap, alt. 1430, 23.XI.68, Col. R.E. Woodruff, *Paxillus jamaicensis* Hincks Reyes-Castillo, det. 88 (3♀♀, 2♂♂ IEXA); Hardwar GAP 7-XII-1975 coll. J.H. Frank. In rotting wood (1 UVGC); Portland Parrish, Hardwar Gap, Topotypes, 23.XI.1968, R.E. Woodruff, *Spasalus jamaicensis* (Hincks), *Paxillus jamaicensis* Hincks det. R.E. Woodruff 1969 (4 UVGC); F. Klages, Holl& Collection, *Paxillus jamaicensis* Hincks Det.: J. Schuster 1988 (1 UVGC).

Distribution. Endemic to Jamaica (Reyes-Castillo & Fonseca 1992, Ivie & Gillogly 1998).

Comments. *Paxillus jamaicensis* was described in *Paxillus*; Reyes-Castillo (1973) transferred it to *Spasalus* and Reyes-Castillo & Fonseca (1992) moved it again to *Paxillus*.

***Paxillus pentaphyllus* (Palisot de Beauvois, 1805)**

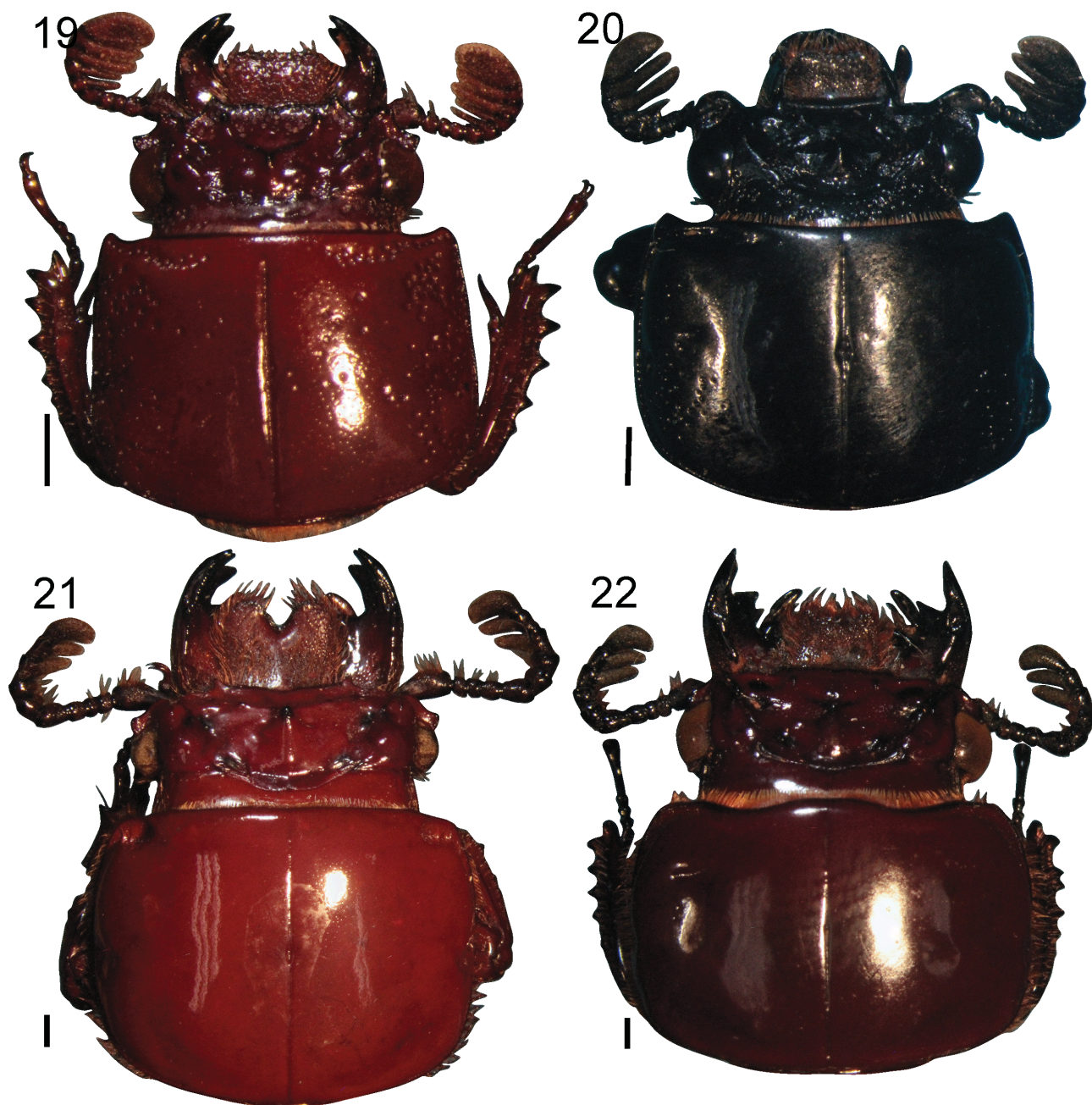
(Fig. 17)

Type locality. Santo Domingo.

Diagnosis. 24.7–26.2 mm total length. Clypeus hidden below frons, not visible dorsally, with anterior angles slightly developed. Frons border straight, without secondary medio-frontal tubercles, with weak notch. Frontal fossae glabrous. Medio-frontal tubercles developed, joined to interior tubercles by a ridge. Internal tubercles smaller than medio-frontal tubercles. Central tubercle with apex not free; basolateral tubercles small but marked. Antennal club with five lamellae, first lamellae reduced. Apex of lacinia unidentate. Mentum with medial base flat and glabrous. Prosternal process pentagonal. Mesosternum glabrous with oval scars. Antero-lateral metasternum and lateral groove pubescent, disc entirely delimited by punctures. Humeri pubescent and epipleura fully pubescent.

Material examined. Six specimens. DOMINICAN REPUBLIC: Engombe, 23.IV.1971, Abud, *Paxillus pentaphyllus* (Beauv.) Reyes-Castillo, det. 88 (1♂ IEXA); La Altagracia, Nisibon, Finca Papagayo, 4–7.iv.2000, blacklight trap, 150', R.E. Woodruff, T.J. Henry/ *Paxillus pentaphyllus* (Beauv.) Det.: Jiménez-Ferbans (1 UVGC). S. Domingo, Higueral, dibujo cabeza Castillo, IX.1988 (1♂ IEXA). HAITI: I. de La Tortue Aux Palmiste, 17.III.1979, Coll. M. Langworthy, T. Dowhan, *Paxillus pentaphyllus* P.B. Reyes-Castillo, det. 1982 (1♀ IEXA); same data, det.: J. Schuster IX.2002 (1 UVGC); Ennery, W.M. Mann, (1 UVGC).

Distribution. Endemic to Hispaniola and I. de La Tortue (Reyes-Castillo & Fonseca 1992, Reyes-Castillo *et al.* 1995, Ivie & Gillogly 1998).



FIGURES 19–22. Head and pronotum, dorsal view. 19. *Spasalus crenatus*. 20. *Popilius tetraphyllus*. 21. *Verres furcilibris*. 22. *Veturius simuosus*. Scale bars: 1 mm.

Spasalus crenatus (MacLeay, 1819)

(Fig. 19)

Type locality. Demerara (=Guyana).

Diagnosis. 17.4–20.0 mm total length. Clypeus hidden below frons, not visible dorsally, with anterior angles well developed. Frons border with a notch and without secondary medio-frontal tubercles. Frontal fossae glabrous. Medio-frontal tubercles developed, not joined to interior tubercles by a ridge. Internal tubercles as large as medio-frontal tubercles. Central tubercle with apex not free; latero-posterior tubercles small but marked. Antennal club with five long lamellae. Apex of lacinia unidentate. Mentum with medial base protruding and glabrous. Prosternal process rhomboidal, acute. Mesosternum glabrous with elongate and marked scars. Antero-lateral metasternum and lateral groove glabrous, disc delimited by punctures from posterior to middle. Humeri glabrous and epipleura with sparse setae basally.

Material examined. 90 specimens. DOMINICA: St. Andrew, 3.VIII.73, Camb., leg., *Paxillus puncticollis* Lepeletiere et Serville (5 IEXA); St. George Parish, Roseau botanical garden, 18.VI.2004, R. Turnbow, *Spasalus* Det.: J.C.S., *Spasalus crenatus* (MacLeay, 1819) Det.: Jiménez-Ferbans, 2012 (1 UVGC). GRENADA, Grand Etang, 12.I.1969, col. R.T. Bell (1 IEXA). GUADELOUPE: Grand-Matouba, 30.VI.1971, col. L. Gruner (24 IEXA); Neuf-Chateau, Sainte Marie, 1.VIII.1971, col. L. Gruner (14 IEXA); same locality and collector, 1.VIII.1971 (2 IEXA). MARTINIQUE: Morne de Golet, 11.8.1975, *Spasalus crenatus* (MacLeay) det. 1998 A. R. Gillogly (4♀ IEXA). PUERTO RICO: El Verde Field Sta. El Verde, P.R. V-18-70. R. Laviane// Under bark of log// *Paxillus crenatus* MacLeay. Det.: R. Lavigne 1970 (2 IEXA); Humacao Dist., Casa Cabuy, Hwy. 191 nr. Florida, 31.VII-2.VIII.1999. J.E. Eger (1 IEXA); Jayuya. 5-III-64, col. G. Halffter (7 IEXA); Lares, 5.IV.47. coll. J.N.A. (1 IEXA); Las Marías, IX, 1940. Mendez (1 IEXA); Luquillo. Exp. Forest, El Verde Station, ex decaying log, 500 m, 4.I.1988, col. J. B. Wallace (8 IEXA); Ponce Rd. 10 Km 24, inside decayed log 600 m, 2.I.1977, J. Micheli, *Paxillus puncticollis* (6 IEXA); same data as before, 3.I.1977, (7 IEXA); same data as before Km 21, 11.IX.1976 (5 IEXA). SAINT LUCIA: Thomazo, 12.IV.1978, Fc. & Camberfort (1 IEXA).

Distribution. Dominica, Dominican Republic, Guadeloupe, Martinique, Puerto Rico, Saint Lucia, Saint Vincent and the Grenadines, and Virgin Islands (Cartwright & Chalumeau 1978; Ivie & Gillogly 1998; Peck 2006, 2009; Galindo-Cardona 2003; Galindo-Cardona *et al.* 2007). Widespread in South America: Argentina, Brazil, Colombia, French Guiana, and Suriname (Reyes-Castillo 1973).

Comments. Luederwaldt (1931) and Ivie & Gillogly (1998) recorded this species from Cuba, but we have never seen specimens from this island. Galindo-Cardona (2003) comments that *S. cretaus* is the only Passalidae in Puerto Rico. Chalumeau & Gruner (1974) noted that it has been collected in rotting logs of *Bursera icica* (Burseraceae).

Tribe Proculini

Popilius tetraphyllus (Eschscholtz, 1929)

(Fig. 20)

Type locality. Guyana.

Diagnosis. 17.0–21.0 mm total length. Anterior border of labrum straight. Clypeus exposed, visible dorsally, with anterior angles well developed. Frontal-clypeal suture present. Frontal fossae punctate and pubescent. Internal tubercles large. Central tubercle with apex not free; latero-posterior tubercles marked, joined by a ridge to central tubercle. Antennal club with three or four lamellae. Apex of lacinia bidentate. Mentum with medial base protruding and glabrous. Prosternal process rhomboidal, acute. Mesosternum glabrous, with weak scars. Antero-lateral metasternum pubescent, lateral groove glabrous, disc delimited by punctures basally. Humeri and epipleura glabrous.

Distribution. Bolivia, Brazil, Colombia, French Guiana, Guyana, Trinidad and Tobago, and Venezuela (Gillogly 2005).

Comments. We did not review material from the Antilles of this species; the diagnosis and measurements are based on Gillogly (2005) and material from Brazil and Guyana deposited in the IEXA collection.

TABLE 1. Species of Passalidae recorded from the Antilles. We only include the oldest references and recent citings that summarize label data for Antilles specimens. *Endemic species to the Antilles. **Species with a South American distribution that are present in Trinidad and Tobago.

Passalidae from Antilles	Reference
<i>Passalus (Passalus) abortivus</i> **	Kaup (1871): Antilles
<i>Passalus (Passalus) bucki</i> **	Trinidad
<i>Passalus (Passalus) coarctatus</i>	Trinidad
<i>Passalus (Passalus) interruptus</i> **	Arrow (1907) Trinidad Schuster (1978): Trinidad
<i>Passalus (Passalus) interstitialis</i>	Kaup (1871): Cuba Arrow (1907): Trinidad, Grenada, Cuba, Jamaica
<i>Passalus (Passalus) punctiger</i>	Arrow (1907): Trinidad, Grenada, Saint Vincent Chalumeau (1978): Saint Vincent Schuster (1978): Grenada
<i>Passalus (Passalus) trinesides</i> *	Martinique, Dominica, Saint Lucia
<i>Passalus (Passalus) unicornis</i>	Percheron (1835): Guadeloupe Arrow (1907): Dominica, Saint Lucia. Chalumeau (1978): Saint Lucia Schuster (1992): Guadeloupe
<i>Passalus (Pertinax) affinis</i> *	Percheron (1835): Dominican Republic Arrow (1907): Santo Domingo, Haiti Reyes-Castillo <i>et al.</i> (1995): Dominican Republic, Haiti
<i>Passalus (Pertinax) antillarum</i> *	Arrow (1907): Grenada Hincks & Dibb (1935)
<i>Passalus (Pertinax) dominicanus</i> *	van Doesburg (1953): Dominican Republic Reyes-Castillo <i>et al.</i> (1995) Dominican Republic
<i>Passalus (Pertinax) latifrons</i> **	Schuster (1992): Tobago
<i>Passalus (Pertinax) pertyi</i> *	Kaup (1869): Cuba García <i>et al.</i> (2009): Holguín, Cuba.
<i>Passalus (Pertinax) doesburgi</i> *	Dominican Republic
<i>Paxillus jamaicensis</i> *	Hincks (1950): Jamaica
<i>Paxillus pentaphyllus</i> *	Palisot de Beauvois (1805): Dominican Republic Reyes-Castillo <i>et al.</i> (1995): Dominican Republic, Haiti
<i>Spasalus crenatus</i>	Arrow (1907): Dominica, Saint Lucia, Nevis (as <i>Passalus puncticollis</i> Lepeletier & Serville) Gravely (1918): Guadeloupe Chalumeau (1978) Saint Lucia (as <i>P. puncticollis</i>) Cartwright & Chalumeau (1978): Dominica (as <i>P. puncticollis</i>) Galindo-Cardona <i>et al.</i> (2007) Puerto Rico
<i>Popilius tetraphyllus</i> **	Gillogly (2005): Trinidad
<i>Verres furcilibris</i> **	Arrow (1907): Trinidad Marshall (2000): Tobago, Trinidad
<i>Veturius sinuosus</i> **	Hunt (1982): Trinidad (as <i>Veturius transversus</i>)

***Verres furcilibris* (Eschscholtz, 1929)**

(Fig. 21)

Type locality. Guyana

Diagnosis. 39.8–43.9 mm total length. Anterior margin of labrum deeply concave, with a “scooped out” excavation in labrum behind concavity of margin. Clypeus exposed, visible dorsally, with anterior angles well

developed. Frontoclypeal suture absent. Frontal fossae smooth and glabrous. Internal tubercles large. Central tubercle with apex not free; basolateral tubercles absent. Antennal club with three short lamellae. Apex of lacinia bidentate. Mentum with medial base protruding and glabrous. Prosternal process rhomboidal, acute. Mesosternum glabrous, without scars. Antero-lateral metasternum and lateral groove pubescent, glabrous; disc delimited by punctures in posterior part. Humeri with sparse setae basally and epipleura glabrous.

Material examined. Seven specimens. TRINIDAD AND TOBAGO: Trinidad: St. Andrew County, 3 mi N of Matura, 27.III.1987, ex palm tree logs on ground, P. Hunter, W.T. Atyeo (3♂♂ IEXA); Nariva Swamp. 26.II.1968, J.G. Rozen, *Verres furciculabris* (Eschscholtz) Reyes-Castillo, det. 1972 (1♂ IEXA); George County, mountains 7 mi N Port of Spain, 26.III.1987, ex decaying log. P. Hunter, W.T. Atyeo (1♀, 2♂♂ IEXA).

Distribution. Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname, Trinidad and Tobago, and Venezuela (Marshall 2000).

Comments. Schuster (1992) described the larvae of this species, based on specimens from Tobago. Hunt (1982) described one new species of nematode from gut of *Verres furciculabris* from Trinidad.

Veturius sinuosus (Drapiez, 1820)

(Fig. 22)

Type locality. Brazil.

Diagnosis. 33–41 mm total length. Anterior margin of labrum slightly concave, without excavation in labrum behind concavity of margin. Clypeus exposed, visible dorsally, with anterior angles well developed. Frontoclypeal suture absent. Frontal fossae smooth and glabrous. Internal tubercles large. Central tubercle with apex not free; basolateral tubercles curved, small, but marked. Antennal club with three short lamellae. Apex of lacinia bidentate. Mentum with medial base protruding and glabrous. Prosternal process rhomboidal, acute. Mesosternum pubescent, without scars. Antero-lateral metasternum and lateral groove pubescent, glabrous, disc not delimited by punctures or reduced punctures basally. Humeri and epipleura glabrous.

Distribution. Argentina, Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Paraguay, Peru, Trinidad and Tobago, and Venezuela (Boucher 2005).

Comments. We did not review material from the Antilles of this species; the diagnosis and measurements are based on Boucher (2005) and material from Brazil and Venezuela deposited in the IEXA collection.

Hunt (1982) described one new species of Nematoda from the gut of *Veturius sinuosus* from Trinidad, citing it as “*Veturius transversus* var. *trituberculatus* (Esch.)”, due to synonymy of *V. sinuosus* with *V. transversus* (Dalman). However, Boucher (2005) revalidated *V. sinuosus*.

Key for the identification of species of Passalidae of the West Indies

1. Clypeus hidden beneath frons, with anterior angles below the mediofrontal teeth 2
- Clypeus exposed dorsally, with anterior angles in front of frons border 18
2. Maxilla with lacinia apex unidentate. Antennal club with five lamellae 3
- Maxilla with lacinia apex bidentate. Antennal club with three lamellae. (*Passalus*) 5
3. Prosternal process rhomboidal. Profemur with marginal groove on the anterior border of the ventral face marked and complete. Body convex, small (length 17.4–20.0 mm). Greater and Lesser Antilles *Spasalus crenatus* (MacLeay)
- Prosternal process pentagonal (Fig. 3D). Profemur with marginal groove on the anterior border of the ventral face absent or not marked and incomplete. Body flattened, medium length (24–29 mm) (*Paxillus*) 4
4. Antennal club with short lamellae, the first lamellae reduced. Profemur without marginal Groove on the anterior border of the ventral face (Fig. 3A). Epipleura glabrous. Jamaica (length 27.2–29.7 mm) *Paxillus jamaicensis* Hincks
- Antennal club with long lamellae, the first not reduced. Profemur with marginal Groove on anterior border of ventral face incomplete. Epipleura entirely pubescent. Hispaniola (length 24.7–26.2) *Paxillus pentaphyllus* (Palisot de Beauvois)
5. Frons border with two secondary tubercles (subgenus *Passalus*). 6
- Frons border straight or almost straight, without secondary tubercles (subgenus *Pertinax*) 13
6. Central tubercle of median frontal structure with apex very free, reaching the anterior border of frons 7
- Central tubercle not free or only slightly free, never reaching the anterior border of frons 9
7. Lateral fossae of pronotum pubescent. Striae 8–10 entirely pubescent. Lesser Antilles (length 36.6–45.0 mm) *Passalus unicornis* LePeletier & Serville
- Lateral fossae of pronotum glabrous. Striae 8 and 9 glabrous, 10 pubescent in basal third (length 34–42 mm) 8

8. Medial base of mentum pubescent. Mesosternal scar slight, densely pubescent. Trinidad (length 34.9–38.3 mm) *Passalus coarctatus* Percheron
- Medial base of mentum glabrous. Mesosternal scar marked, glabrous. Martinique, Saint Lucia, and Dominica (length 40.5–41.6 mm) *Passalus trinesides* Boucher
9. Mediofrontal secondary teeth basally contiguous. Frontal fossae pubescent. Trinidad (length 28.2–30.6 mm) *Passalus abortivus* Percheron
- Mediofrontal secondary teeth basally separated. Frontal fossae glabrous 10
10. Body flattened. Central tubercle short, apex not free 11
- Body convex. Central tubercle long, apex free 12
11. Epipleura 2/3 or more pubescent. Medium length (29–34 mm). Greater and Lesser Antilles *Passalus interstitialis* Eschscholtz
- Epipleura pubescent only on basal third. Short length (24–30 mm). Trinidad *Passalus bucki* Luederwaldt
12. Marginal groove of last abdominal sternite incomplete. Trinidad (length 44.2–50.9 mm) *Passalus interruptus* (Linnaeus)
- Marginal groove of last abdominal sternite complete. Greater and Lesser Antilles (length 31.5–38.3 mm) *Passalus punctiger* LePeletier & Serville
13. Length greater than 39 mm 14
- Length less than 31 mm 15
14. Mesepimeron, metasternal grooves, humeri, and epipleura pubescent. (length 42.5–48.6 mm). Hispaniola *Passalus affinis* Percheron
- Mesepimeron, metasternal grooves, humeri, and epipleura glabrous (length 39.5–40.9 mm). Cuba. *Passalus pertyi* (Kaup)
15. Mesosternal scar present. Body length short (21.5–22.5 mm). Grenada *Passalus antillarum* (Arrow)
- Mesosternal scar absent. Body length medium to large, greater than 26 mm. 16
16. Pronotal arms glabrous in the half closest to prosternal process. (Length 29.3–30.8 mm). Trinidad, Tobago. *Passalus latifrons* Percheron
- Pronotal arms pubescent throughout. 17
17. Internal tubercles large, apices free. Clypeus slightly visible dorsally. (Length 27.9–30.6 mm). Hispaniola *Passalus dominicanus* van Doesburg
- Internal tubercles small, apices not free. Clypeus not visible dorsally. (Length 26.6–28.4 mm). Hispaniola *Passalus doesburgi* (Boucher)
18. Anterior border of labrum deeply concave, concavity excavated behind border. (Length 39.8–43.9 mm). Tobago, Trinidad ... *Verres furcilibris* (Eschscholtz)
- Anterior border of labrum straight or slightly convex, without excavation behind anterior border 19
19. Frontoclypeal suture present and strong. Anterior pronotal border straight. (Length 17–21 mm). Trinidad *Popilius tetraphyllus* (Eschscholtz)
- Frontoclypeal suture absent. Anterior pronotal border sinuous (Length 33–41 mm). Trinidad *Veturius sinuosus* (Drapiez)

Discussion

Chalumeau (1983), Reyes-Castillo *et al.* (1995), and Ivie & Gillogly (1998) made important contributions to refine the list of West Indian Passalidae, eliminating records of species not found in the region such as *Paxillus leachi* MacLeay, *Passalus coniferus*, *Passalus binominatus* Percheron, *Passalus mucronatus* Burmeister, *Passalus hubneri* Kuwert, and *Passalus simulans* Kuwert. Another species that must be verified using type specimens is *Spasalus robustus* Percheron as it was described without a precise locality. Schuster (1992) described the larva of this species based on specimens from Tobago, but Luederwaldt (1931) and Hincks & Dibb (1935) cite it only from the southern half of South America (Argentina, Brazil, and Paraguay). Schuster (1992) commented that “This species is described in Costa & Fonseca (1986). Differences in size and setal pattern suggest that 1 of us is dealing with a different species”. It is likely that *S. robustus* *sensu* Schuster (1992) is actually another species.

Trinidad and Tobago were connected to South America until 10,000–14,000 years ago (Peck *et al.* 2002), resulting in a similar faunistic composition with northeastern South America. For this reason, many studies do not consider them in their analysis of West Indian biota. Excluding these islands, the Antilles possess a reduced passalid fauna compared to other Neotropical regions and the largest islands have fewer species than regions of equal size in South America (Reyes-Castillo *et al.* 1995); nevertheless, this could reflect a sampling deficiency for some of them, such as Cuba, a large island with only three species recorded.

As Liebherr (1988) indicated for diverse groups of insects, Antillian Passalidae exhibit an obvious affinity with the Central and, especially, South American faunas. Hedges (1996) also referred to a similar pattern for non-flying vertebrates of the Antilles, indicating that 73% of the vertebrate species are endemic, as found in some insect groups (Liebherr 1988). Passalidae reaches 50% endemism, excluding Trinidad and Tobago.

Hedges (2001) suggested that the high Antillean richness and endemism is a product of dispersal events, based

mostly on divergence times estimated by molecular data suggesting Cenozoic colonization when land connection existed between the Antilles and South America. Dispersion could explain the presence of passalids on some volcanic islands, such as Dominica, that have been available for colonization only since the late Miocene (Hedges 2001). Nevertheless, except for *Passalus antillarum*, all the Antillean passalid endemics are concentrated in the Greater Antilles, increasing the probability of a vicariant origin of this biota.

During part of the late Mesozoic and early Tertiary, the archipelago of the Protoantilles connected South and North America. They later (middle and late Tertiary) moved towards the northeast and consolidated the Antilles (Rosen 1975). It is probable that these Protoantilles were colonized by South American passalids, allowing them to reach North America. This would explain the finding of a fossil, *Passalus indormitus* Cockerell, in late Oligocene deposits of Oregon (Reyes-Castillo 1977). Following this reasoning, the Antillean endemic passalids could represent paleoendemisms, products of an early colonization of the Protoantilles by South American elements that remained isolated since then. This hypothesis should be tested by phylogenetic studies applying both molecular and morphological analyses to confirm migration or vicariant processes and assigning diversification times.

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